

Agr. Expt. Sta. Bull. no. 24), 469 (1892), that name is invalid, because a *nomen nudum*.

In RHODORA, li. 71 (footnote) (1949), I cited the name *Convolvulus sepium*, var. *repens* as starting with Coleman. Miss Stone notes that Coleman's initial "C" stood for *Calystegia*. The author of *Convolvulus sepium*, var. *repens* is Gray.—M. L. FERNALD.

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CONTRIBUTIONS FROM THE GRAY HERBARIUM OF  
HARVARD UNIVERSITY—NO. CLXX

THE AMERICAN BARBISTYLED SPECIES OF  
TEPHROSIA (LEGUMINOSAE)

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(Plates 1152–1155)

INTRODUCTION

ALTHOUGH the name *Tephrosia* has been used for a genus of moths, it is perhaps more familiar to biologists for a large genus of several hundred species of plants, members of the Tribe Galegeae, Family Leguminosae, widely distributed in warm-temperate and tropical regions. Many of these species produce rotenone and related compounds, so that the group is not only of economic importance as a potential source of insecticides non-poisonous to mammals, but also of ethnological interest in connection with the capture of fish by poisoning. Nevertheless, since the time of DeCandolle no attempt has been made to consider the genus as a whole and even regional monographs have been few and, for the most part, inadequate. To those who have attempted to determine specimens on the basis of existing treatments the need for a revision of the genus should be evident. The high percentage of misidentified specimens in herbaria and the confusion in anthropological, entomological and chemical literature in connection with the use of various species of *Tephrosia* as fish-poisons and insecticides are further indications of the desirability of re-examination of the genus. The large number of species involved, however, and the lack of workable, well-established subgeneric divisions necessitates a piecemeal approach on a regional basis.

Although it was originally intended to attempt a taxonomic revision including all of the North American species, the problem was later recast to deal with only a part of the species of both American continents. This change in emphasis resulted when it became evident that the New World species of *Tephrosia* fall into two rather natural groups: those with glabrous styles and those with bearded or barbate styles. The species with glabrous styles make up a particularly vexing assemblage which it has been impossible to revise in a consistent manner with the information now available. The other group, however, is more amenable to revision, contains a wide range of morphological types and offers a more suitable point for attacking the genus. This paper is limited, therefore, primarily to a survey of the larger, barbistyled group which in the New World occurs principally in North America, with two representatives extending into South America. Various references are made, however, to species with glabrous styles, while much of the general discussion applies to all of the American species; and a list of the names excluded by this style-character is placed at the end of the revision.<sup>1</sup>

Some ninety described species and varieties and many more nomenclatural combinations are involved in the barbistyled group, but a high mortality of binomials in this work leaves the New World with 45 endemic species (including 7 previously undescribed), 2 naturalized exotics and 2 apparent waifs. I do not think, however, that this is needless "lumping," but that specific boundaries are, as a result, more natural and distinct, with the species themselves established on more stable bases than in the past, even though there remain many points of doubt and much to be done, while the interrelationships of most species are anything but clear.

Although almost everyone will agree that in any taxonomic study of a group of plants it is desirable to use information derived from all aspects of the plants and their biology, with some groups certain lanes of approach are, of necessity, either closed or limited until other obstacles are cleared away. It is obvious that it is first necessary to work out a system of interrelationships based on the accumulated information in herbaria with such

<sup>1</sup> For clarity all species belonging to the glabrous-styled group will be marked by an asterisk (\*) wherever mentioned in connection with barbistyled species.

geographical and ecological data as may be available. With this as a beginning, further enlightenment may be sought with the aid of more extensive field-study of populations and their ecology, along with anatomical, cytological, genetic and physiological studies. With the additional information thus painfully obtained, the original taxonomic treatment may be remodeled into a more natural one. It is essential first, however, to have some rough outline from which to work.

The revision of the New World barbistyled *Tephrosias* attempted here is in the nature of that rough outline with a few beginnings of more detailed studies. The approach has been primarily morphological and geographical, with herbarium-specimens as a basis. I have, however, taken the welcome opportunity of escaping from the herbarium to study in the field a number of the species of the United States and Mexico, so that my acquaintance with the genus is not entirely second-hand. A beginning has also been made in the use of cytological data and some anatomical information has been obtained. Unfortunately, the inaccessibility of the regions in which many of the plants grow, the impossibility of obtaining seeds of more than half of the species, the relatively slow growth, deep tap-roots and perennial habit and, particularly, the difficulties of cultivation of most species in the northern part of the United States have precluded environmental manipulations and genetic experiments. In addition, a number of the species from the poorly explored mountains of western Mexico are represented by only one or a few collections, mostly with scanty field-data, so that the distribution, range of variation, flower-color, fruit and seeds are poorly understood or completely unknown. This beginning is presented, however, without apologies, but with the usual hope that it will indicate some of the problems involved and lead to further, more complete, studies of the genus.

#### ACKNOWLEDGMENTS

It is a pleasure to acknowledge the assistance of the many people without whose interest this study would never have been brought to its present state. I am greatly indebted to Professor M. L. Fernald who suggested the problem and under whose direction the work was begun. The revision has been completed

through the guidance, helpful criticism and enthusiastic interest of Professor Lincoln Constance to whom I am especially grateful. Professor I. W. Bailey has displayed a keen interest in the morphological and anatomical aspects of the work and has kindly demonstrated various techniques for me. The late Mr. C. A. Weatherby gave generously, as always, his kindly advice and assistance in nomenclatural problems. I am grateful to Dr. Bernice G. Schubert, Dr. R. C. Foster, Dr. H. E. Moore, Jr., and Miss Ruth D. Sanderson, of the Gray Herbarium, for their assistance with many perplexing matters which have arisen. Dr. Earlene Atchison, of the University of North Carolina, suggested the cytological technique used and gave me much helpful advice on this subject. Dr. E. Lucy Braun, of the University of Cincinnati, has kindly allowed me to study the collections of *Tephrosia* in her private herbarium and I have had the privilege of examining the herbarium of Mr. Ira W. Clokey deposited at the University of California. Mr. A. G. Olsen and Mr. H. N. Cooledge, Jr., aided materially in the preparation of some of the maps. At the University of California, where the work was completed, I have had the welcome advice and help of many friends. The careful collections kindly made by Miss Annetta Carter in Baja California in the spring of 1949 have been very helpful in resolving several problems.

Particular acknowledgment is due for the assistance given me by Harvard University through an Atkins Scholarship in 1947 and a Parker Fellowship in Biology in 1948-49. The first enabled me in the summer of 1947 to undertake field-studies with Dr. and Mrs. I. D. Clement on the southeastern Coastal Plain and then in Cuba, where a month was spent at the Atkins Garden and Research Laboratory of Harvard University at Soledad, near Cienfuegos. I am indebted to Dr. A. G. Kevorkian, then Director, for many favors during the stay at Soledad. As a Parker Fellow in 1948, I was able to spend two months in field-study in Mexico with Dr. H. E. Moore, Jr., now of the Bailey Hortorium, Cornell University. Data and seeds from numerous species of *Tephrosia* studied in the western Sierra Madre have resulted in the clarification of a number of problems.

The curators of the following institutions (designated in the

text by the initials here given<sup>1</sup>) have generously permitted me to borrow extensively from the abundant material in their care:

A	Arnold Arboretum, Harvard University
CAS	California Academy of Sciences
DS	Dudley Herbarium, Stanford University
DUKE	Duke University
F	Chicago Natural History Museum
FLAS	Agricultural Experiment Station, University of Florida
GA	University of Georgia
GH	Gray Herbarium, Harvard University
ISC	Iowa State College
K	Royal Botanic Gardens, Kew
KSA	Kansas State Agricultural College
KY	University of Kentucky
MEXU	Instituto de Biología, Universidad Nacional de México
MIAMI	Buswell Herbarium, University of Miami, Coral Gables
MO	Missouri Botanical Garden
NEBC	New England Botanical Club
NY	New York Botanical Garden
OKL	University of Oklahoma
PH	Academy of Natural Sciences of Philadelphia
PHBC	Philadelphia Botanical Club
POM	Pomona College
SMU	Southern Methodist University
TENN	University of Tennessee
TEX	University of Texas
UC	University of California (including the Clokey Herbarium)
US	United States National Herbarium
WVA	West Virginia University

#### HISTORICAL ACCOUNT

The confused history of *Tephrosia* as a genus began with Linnaeus who, in the first edition of *Species Plantarum* (1753), set off the genus *Cracca* with six species, all of which are currently recognized as species of *Tephrosia*. Later, however, he doubted the distinctness of *Cracca* and merged it with *Galega* (Linnaeus 1759, p. 1172),<sup>2</sup> where it remained in obscurity until resurrected by Kuntze in 1891.

After Linnaeus numerous species were described under *Galega* (which became more or less a catch-all) and at least four other generic names were applied to plants now included in *Tephrosia*. The genus *Tephrosia* itself was proposed as segregate from *Galega* by Persoon (1807, pp. 328–330) who transferred into it a rather heterogeneous series of species, including the original *Craccae* of Linnaeus (and related species) as well as plants now

<sup>1</sup> Most of the abbreviations adopted are those suggested by Lanjouw (1939, 1941).

<sup>2</sup> In a footnote he explains, "Galegam 770 & Craccam 795 genere sub eodem comprehendendi docuere recentiores observationes".

recognized as belonging to very different genera. Although *Tephrosia* Pers. was thus a superfluous name (including as it did *Cracca* L.), it was adopted by most writers and the extraneous elements gradually removed to other genera, leaving the genus taxonomically essentially as now understood and nomenclaturally synonymous with *Cracca* L.

Some of the last of the discordant elements included in *Tephrosia* by Persoon were removed by Bentham (1853) who erected for them an entirely new genus *Cracca*<sup>1</sup>, based on *Galega caribaea* Jacq., a plant morphologically quite different from true *Tephrosia* Pers. (*Cracca* L.). The situation was still further complicated by the appearance of a third genus *Cracca* when Alefeld (1861), agreeing with Grenier and Godron (1848), revived the pre-Linnaean *Cracca* Riv. (1691)<sup>2</sup> for a portion of *Vicia* L. Adopting the view that this earlier use of the name necessitated new names for both *Cracca* L. and *Cracca* Benth., Alefeld (1862) continued the use of *Tephrosia* Pers. for the former and proposed a new name, *Benthamantha*, for the latter. Most authors, however, either overlooked or ignored Alefeld and continued to use *Tephrosia* Pers., *Cracca* Benth. and *Vicia* L. (*sens. lat.*). Finally, to make the confusion complete, Kuntze (1891), on the basis of priority, adopted *Cracca* L. for *Tephrosia* Pers., transferred all the known species of *Tephrosia* to that genus and, apparently not knowing of Alefeld's *Benthamantha*, proposed yet another name, *Brittonamra*, for *Cracca* Benth.

*Cracca* [Riv.] Medic. has not seriously been considered as a genus since Alefeld, but *Cracca* L. and the very different *Cracca* Benth. have inevitably been badly tangled nomenclaturally. Although *Tephrosia* Pers., which had been widely used for almost a hundred years, was conserved over both *Cracca* L. and *Cracca* Medic. by the International Botanical Congress of 1905 and was again included in the list of *nomina conservanda* in 1910, adherents to the American Code continued to recognize *Cracca* L. as the proper name for the genus. *Cracca* Benth.,

<sup>1</sup> Although the name is usually cited as of Benth. ex Oerst., both Bentham and Oersted are the authors of this paper. The proper citation is *Cracca* Benth. ex Benth. & Oerst.

<sup>2</sup> Although these authors attributed the genus to Rivinius, under the present rules this is properly *Cracca* Medic. Vorles. Churpf. Phys. Ges. 2: 359. 1787, which was proposed as a segregate from *Vicia* L., based on *V. Gerhardi* Jacq., *V. benghalensis* L. and a new species, *C. syriaca*. It is treated by most authors as a section of *Vicia* L. or as a synonym under that genus.

twice a later homonym, became *Benthamantha* Alef. However, with the demise of the American Code the conservation of *Tephrosia* was again confirmed (Briquet 1935) and has been generally accepted.

*Cracca* Benth. has now been proposed and accepted for conservation (Rehder et al. 1935; Sprague 1940), but has not yet been acted upon by a Botanical Congress. The proposed conservation of this name which, although rather generally accepted until fifty years ago, has since become surrounded by an aura of confusion, at least in the United States, would not seem to contribute to nomenclatural clarity. It would appear better to eliminate the name completely and to continue to use *Benthamantha* Alef. There could then be no doubt as to which genus was intended. It is to be hoped, however, that, should *Cracca* Benth. be approved as a conserved name by the next International Botanical Congress, the confusion will abate in time.

The nomenclatural confusion aside, *Tephrosia*, as a genus, has been the subject of relatively few treatments. No attempt has been made since A. P. DeCandolle (1825, pp. 248–256) to monograph the genus on a world-wide scale, although several regional works have treated it in part. E. G. Baker (1926) revised the species of tropical Africa, recognizing 146 species, many of which were based on variable pubescence-characters. According to an excellent recent monograph (Forbes 1948), 67 species are known from South Africa. The most recent monograph of the Australian species is that of Domin (1926, pp. 746–756) who concluded that 23 species occur in that continent. The Asiatic species have not yet, to my knowledge, been treated as a group.

Although numerous short papers concerned with North American *Tephrosias* have been published, only four have dealt with these at any length. The first was a "Revision of the North American Species of *Cracca*" by Anna Murray Vail (1895). She concluded that 14 species and 3 varieties occurred in "North America" (i. e., the United States). Four years later B. L. Robinson (1899), dissatisfied with Miss Vail's work, published a somewhat more useful "Revision of the North American Species of *Tephrosia*," still restricting North America to the United States and including 12 species and 5 varieties. A further treat-

ment of importance was not forthcoming until Standley (1922) brought together in his "Trees and Shrubs of Mexico" much of the available information concerning 26 Mexican species.

It remained, however, for Rydberg (1923) to monograph the species occurring in North America, including the West Indies. This work, in which he treated 72 species, 16 of which were described as new, is far from satisfactory, for many of the specific descriptions are little more than rewordings of the original, usually inadequate diagnoses, the keys contradict both themselves and the descriptions, and the specific lines are often finely drawn and based entirely on such inconstant characters as pubescence of the vegetative organs. Rydberg's herbarium annotations follow the outlines of his monograph and indicate that he did not clearly understand many of the entities with which he was dealing. However, handicapped though he was by the relatively few specimens then available and by his extreme tendency toward "splitting", his work remains to date the only outline of the North American species. About 50 of the 72 species given by Rydberg appear to represent "good" species.

Various notes concerning South American species have been published, but apparently nothing dealing expressly with these as a group has appeared. Bentham in Martius, Fl. Bras. **15** (1): 46-50. 1859, recognized 7 species in Brazil. Comments on the genus in Brazilian Amazonia are included in Ducke's work (1939) on the legumes of that region and Burkart (1943) records 3 species from Argentina in his study of the legumes of that country. A number of species were dismembered by Chodat and/or Hassler in various publications.

#### ECONOMIC IMPORTANCE

Various species of *Tephrosia* have been used as fish-poisons in the Americas, Africa, Asia and Australia. It is remarkable that primitive peoples in such isolated parts of the world, lacking any apparent communication with one another, have discovered and domesticated species of the same genus for the same purpose, the poisoning of fish. The species most frequently mentioned in this connection are *Tephrosia Sinapou* in the Caribbean area and South America, *T. multifolia* and *T. Sinapou* in Central America,



*T. Vogelii* and *T. macropoda* in Africa, and \**T. rosea* and \**T. astragaloides* in Australia.

An early account of fish-poisoning with *Tephrosia Sinapou* in Jamaica illustrates the general method used in capturing fish:

The leaves and branches of this plant, being well pounded and thrown into any river, pond, or creek, are observed to infect the waters very soon: by which all the fish are immediately intoxicated and rise and float upon the surface, as if they were dead; from whence they are easily taken. But most of the large ones that are left recover from this trance, after a short time: tho' the greatest part of the small fry perish on those occasions (Browne 1756, p. 296).

Although in this instance the shoots are toxic to fish, in other species only the roots are used, the foliage being completely harmless. *Tephrosia Sinapou* appears to have been widely cultivated in the Caribbean region in pre-Columbian times and even later. Browne (1756) notes that it was "introduced to *Jamaica* from the main", and was "cultivated in many parts of the island, on account of its intoxicating qualities". With the near extinction of the Indians of the Caribbean, however, the plant has become rare in the West Indies, although it is still widely cultivated in South America as a fish-poison.

Some species have long been used by primitive peoples as insecticides, as well as fish-poisons, and in recent years have come to the attention of economic entomologists and chemists. The toxic qualities of these plants are due to the presence of rotenone, deguelin and related compounds which are chemically identical with those found in *Derris* and *Lonchocarpus*, the commercial sources of rotenone. They are not, however, present in such large quantities as in those plants, and this factor limits the commercial exploitation of *Tephrosia* species at the present time. The maximum rotenone- and deguelin-content of *Tephrosia virginiana*, for example, is about 4 per cent, whereas *Derris* and *Cube* often contain 10 per cent or more (Roark 1937).

Nevertheless, rotenone has become so important as an insecticide non-poisonous to mammals that extensive surveys have been conducted by the U. S. Department of Agriculture to determine the feasibility of cultivating native species as commercial sources. In 1934 and 1935, many of the species of the southeastern United States were tested, but only *Tephrosia virginiana* (including *T. latidens*) appeared to be promising (Sievers, Russell et al.

1938). As a result, cultural experiments in the United States have been confined to this species.

In the course of one of these surveys (1935), plants of *Tephrosia virginiana* from many localities from Virginia southward and westward were tested for the presence of rotenone. Large areas were found to lack completely any toxic plants, but plants with relatively high rotenone content were found in light, sandy soils in northeastern and western Florida, and in northeastern Texas within a narrow belt extending some 300 miles between Caldwell and Harrison counties. Secondary districts were located in Georgia, Louisiana, Texas and Oklahoma. The evidence accumulated at that time suggested that the presence of toxic substances was controlled by genetic factors, the expression of which was affected by the environment, particularly edaphic conditions (Sievers, Russell et al. 1938). Transplant-experiments have since indicated that the controlling factors are indeed hereditary, for plants with high rotenone-content retain their toxicity when transferred to a region yielding only mediocre material, and also when transferred from one soil-type to another. It has also been shown that highly toxic plants tend to produce offspring of similar toxicity (Little 1942).

*Tephrosia virginiana* responds well to cultivation in sandy soils, requiring little attention and giving economically promising yields. The roots, in addition to producing rotenone<sup>1</sup>, harbor nitrogen-fixing bacteria. The leaves and stems of this species are non-toxic and have some value as hay.

A great mass of technical literature concerning the use of *Tephrosia* as an insecticide has accumulated in the last 20 years. The portion up to 1937 has been thoroughly reviewed by Roark (1937). A more general account up to 1941 of the literature concerning plants of possible insecticidal value has been given by McIndoo (1945).

*Tephrosia* species have also been utilized in tropical agriculture as green manures, cover-crops, soil-binders and contour-hedges. Most of the species so used are native to the Eastern Hemisphere, although "*Tephrosia toxicaria*" (either *T. Sinapou* or *T. multifolia*) has been grown as a green manure in the Nether-

<sup>1</sup> Rotenone is found concentrated in the xylem and not in the bark. All roots contain the same proportion of toxic substances regardless of size (Sievers, Russell et al. 1938).

lands Indies. \**Tephrosia noctiflora* appears to have been introduced into the West Indies as a cover-crop, as perhaps was *T. candida*.

Various medicinal properties have been assigned to *Tephrosia* species. Among these may be mentioned the use of the roots of *T. virginiana* as a vermifuge by the Indians of eastern North America (Griffith 1847; Rafinesque 1830). The purgative properties of \**T. Senna* HBK. (*T. cathartica*) are further commemorated by the common name "Wild Senna" in the British West Indies.

The ornamental possibilities of *Tephrosia* have been little explored, although *T. Vogelii* is cultivated in tropical Africa both as a fish-poison and as an ornamental shrub. *Tephrosia macrantha*, a shrub of western Mexico with large attractive flowers and a long blooming period, would probably make a very desirable cultivated plant in frost-free regions.

#### CYTOLOGY

In addition to the usual morphological characters, an attempt was made to utilize the chromosome-numbers of some of the species of *Tephrosia* as a systematic criterion. More data of this type seemed to be particularly desirable since Senn (1938), in reviewing the chromosomal relationships within the Leguminosae, had indicated that the genus was evidently in need of careful chromosomal, as well as taxonomic, study.

Efforts were made in the summer of 1947 to secure counts of meiotic chromosomes, particularly those of \**Tephrosia cinerea*, at the Atkins Garden and Research Laboratory at Soledad, Cuba. These attempts were all unsuccessful, probably because of the sporadic flowering of the inflorescence. The available species of the southeastern United States proved equally difficult. In consequence, chromosome counts from root-tips have been relied upon exclusively.

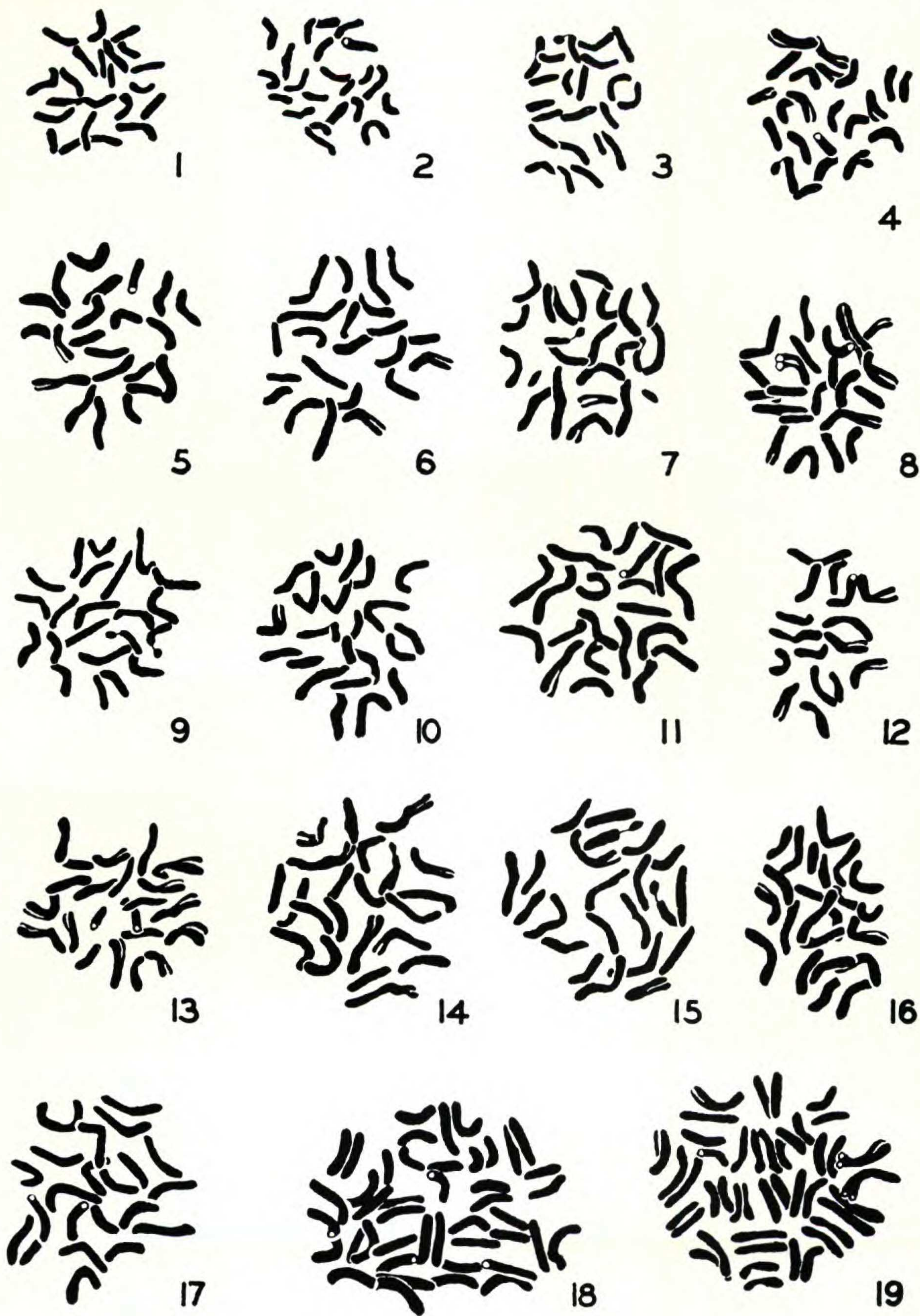
Mature seeds of seven species of *Tephrosia* were collected in the southeastern states and seeds of \**T. cinerea* in Cuba in 1947. In 1948, 3 more species were added from Texas and Mexico. At Soledad fresh, nearly mature but still quite green seeds of \**T. cinerea* germinated immediately in moist Petri dishes, producing vigorous root-tips. In addition, seeds taken from herbarium-specimens have, in many instances, germinated readily. Perma-

ment slides were prepared<sup>1</sup> and chromosome-counts obtained for 27 species. The diploid number is 22 in all. (See Table 1 and Plate 1152).<sup>2</sup>

The chromosome-numbers of only two species have been recorded previously. These are "*T. Hookeriana* W. & A." (probably = *T. villosa* (L.) Pers.),  $n = 16$ , according to Kawakami (1930) and *T. virginiana* (L.) Pers.,  $n = 11$ , reported by Senn (1938, p. 231). The occurrence of these two numbers within the genus was pointed out by Senn as remarkable, particularly since 11 was a number unknown elsewhere within the Tribe Galegeae, 8 being the basic number of most genera. Since then, however, 13 species with 11 pairs of chromosomes have been reported in *Astragalus* (Vilkomerson 1943), a genus previously believed to have only 7 and 8 as the basic numbers, so that the occurrence of 8 and 11 in *Tephrosia* would not necessarily be particularly remarkable. The counts of 27 species of *Tephrosia*, all with 22 somatic chromosomes, suggest, moreover, that the genus is probably very uniform in chromosome-number and strongly indicate that the reported haploid number of *T. Hookeriana* is erroneous. Since the species counted represent a wide range of morphological types, including three Old World species (one presumably a close relative of *T. Hookeriana*), it is likely that these results are fairly conclusive, except for the possibility of polyploid species. To

<sup>1</sup> The seed-coats of dry, mature seeds were sterilized by immersion in 70 per cent alcohol for a few minutes and scarified with a scalpel. The seeds were then rinsed in sterile distilled water and placed on moist filter-paper in sterile Petri dishes. Imbibition of water took place rapidly and germination often followed overnight. Root-tips were stained whole by the Feulgen technique following Belling's or Randolph's fixative, embedded in paraffin via ethyl alcohol and chloroform, sectioned at 10 microns, affixed to slides, passed through xylene to remove the paraffin and finally mounted in balsam. Good results are difficult to obtain in this group with any of the various smearing or "squashing" techniques. Drawings of the chromosomes were made with camera lucida, oil-immersion objective (90x) and 20x compens oculars. Counts are documented by specimens in the herbaria indicated in Table 1.

<sup>2</sup> PLATE 1152. Somatic Chromosomes of *Tephrosia* and *Sphinctospermum*. Mitotic figures from root-tips. Figure 4 ca. 2750 X, all other figures ca. 2600 X. All documenting specimens in (GH). 1. \**Tephrosia vicioides* (Purpus 8171); 2. \**T. tenella* (Gentry 4684); 3. \**T. noctiflora* (Archer 2557); 4. \**T. angustissima* (Wood & Clement 7492); 5. *T. virginiana* (Wood & Clement 7605); 6. *T. Sinapou* (Pringle 11436); 7. *T. Conzattii* (Hinton 6998); 8. *T. foliolosa* (Gentry 5279); 9. *T. nitens* (Hinton 11037); 10. *T. belizensis* (Schultes & Reko 552); 11. *T. spicata* (Wood & Clement 7531); 12. *Sphinctospermum constrictum* (Gentry 4676); 13. *T. hispidula* (Wood & Clement 7194); 14. *T. florida* (Wood & Clement 7596); 15. *T. chrysophylla* (Wood & Clement 7172a); 16. *T. Rugelii* (Wood & Clement 7512); 17. *T. florida* (topotype of *T. gracillima*) (Wood & Clement 7202); 18. *T. chrysophylla*, tetraploid cell (Wood & Clement 7525a); 19. *T. Rugelii*, tetraploid cell (Wood & Clement 7512).



EXPLAINED IN FOOTNOTE, P. 204

TABLE 1  
Chromosome-Numbers of *Tephrosia*, *Cracca* and *Sphinctospermum*

Species	2n	Collection	Year	Locality
<i>T. multifolia</i>	22	Rose, Standley & Russell 14227 (GH)	1910	Nayarit
	22	Calderón 2611 (F)	1933	El Salvador
<i>T. foliolosa</i>	22	Gentry 5279 (GH)	1939	Durango
<i>T. Sinapou</i>	22	Pringle 11436 (GH)	1903	Jalisco
<i>T. leiocarpa</i>	22	Gentry 4894 (GH)	1939	Sonora
<i>T. Conzattii</i>	22	Hinton 6998 (GH)	1934	México (State)
	22+2f			
<i>T. virginiana</i>	22	Wood & Clement 7605 (GH)	1947	South Carolina
	22	7613 (GH)	1947	North Carolina
<i>T. onobrychoides</i>	22	Moore & Wood 3616 (GH)	1948	Texas
<i>T. rhodantha</i>	22	Hinton 11641 (GH)	1937	Guerrero
<i>T. cana</i>	22	Carter, Alexander & Kellogg 2406 (UC)	1947	Baja California
	22	Gentry 4366 (DS)	1939	Baja California
<i>T. Palmeri</i>	22	Gentry 3718 (MO)	1938	Baja California
<i>T. Rugelii</i>	22	Wood & Clement 7170 (GH)	1947	Florida
		7512 (GH)	1947	Florida
<i>T. spicata</i>	22	Wood & Clement 7178 (GH)	1947	Florida
	22	7531 (GH)	1947	Florida
	22	7608 (GH)	1947	North Carolina
<i>T. hispidula</i>	22	Wood & Clement 7194 (GH)	1947	Florida
	22	7547 (GH)	1947	Florida
<i>T. florida</i>	22	Wood & Clement 7089 (GH)	1947	South Carolina
	22	7202 (GH)	1947	Florida
	22	7527 (GH)	1947	Florida
	22	7532 (GH)	1947	Florida
	22	7560 (GH)	1947	Georgia
	22	7565 (GH)	1947	Georgia
	22	7596 (GH)	1947	South Carolina
	22	7598 (GH)	1947	South Carolina
	22	7607 (GH)	1947	North Carolina
<i>T. chrysophylla</i>	22	Wood & Clement 7172a (GH)	1947	Florida
	22	7525a (GH)	1947	Florida
<i>T. Lindheimeri</i>	22	Moore & Wood 3617 (GH)	1948	Texas
<i>T. potosina</i>	22	Moore & Wood 3618 (GH)	1948	Nuevo León
<i>T. nitens</i>	22	Hinton 11037 (GH)	1937	Guerrero
<i>T. belizensis</i>	22	Schultes & Reko 552 (GH)	1939	Oaxaca
<i>T. grandiflora</i>	22	Orcutt 3235 (UC)	1927	Jamaica
<i>T. Vogelii</i>	22	No voucher; identified from seeds only, but these unmis- takable.	1946	Cultivated, Bianchi, Guatemala
* <i>T. cinerea</i>	22	Wood 7537 (GH)	1947	Cuba
* <i>T. Senna</i>	22	Rose et al. 3228 (GH)	1913	St. Kitts, British West Indies
* <i>T. tenella</i>	22	Gentry 4684 (GH)	1939	Sonora
* <i>T. angustissima</i>	22	Wood & Clement 7492 (GH)	1947	Florida
* <i>T. vicioides</i>	22	Purpus 8171 (GH)	1918	Veracruz
* <i>T. noctiflora</i>	22	Archer 2557 (GH)	1934	Cultivated, British Guiana
<i>Cracca</i> sp.	16	Hinton 8740 (GH)	1935	México (State)
<i>Sphinctospermum</i> <i>constrictum</i>	16	Gentry 4676 (GH)	1939	Sonora

\* Styles glabrous.

date, no polyploids have been found, although a few tetraploid cells were encountered in the roots of *T. chrysophylla*, *T. florida* and *T. Rugelii* (Pl. 1152, fig. 18, 19). Such polysomatic cells have been found more or less irregularly, both in the roots of a number of leguminous genera (Atkinson 1948; Vilkomerson 1943) and in various tissues of other families as well, and may be a normal feature of differentiated tissues (Huskins 1948).

The apparent uniformity of chromosome-number in *Tephrosia*, at least in the Western Hemisphere, is disappointing at the species-level, but is interesting as a generic character. Few of the supposedly related genera have been studied cytologically, but two species of *Galega* have been reported with 8 pairs of chromosomes (Kreuter 1929, 1930; Senn 1938). A single species of *Cracca* and the monotypic *Sphinctospermum* also have 8 pairs, although neither of these genera is particularly closely related to *Tephrosia*. The presence of 8 pairs of chromosomes in *Sphinctospermum* is especially interesting, since this plant was originally described as a *Tephrosia* by Sereno Watson. Rose erected a new genus for it on morphological grounds; the chromosome-numbers strengthen this already strong segregation. In both morphology and chromosomes it is much more closely related to *Cracca* Benth. than to *Tephrosia*.

With the amount and type of material now available it seems unwise to attempt to utilize chromosome-morphology as a comparative character. From a glance at Plate 1, however, it will be evident that the chromosomes of at least some of the glabrous-styled species are noticeably smaller than those of barbistyled species and that satellites are present on two chromosomes. Unfortunately, although the satellites are large, they are seldom visible, even in species in which they have definitely been observed. It may also be noted that absolute chromosome-size varies considerably from one cell to another within the same root-tip. In addition, one possible example of ageing in 15-year-old seeds of *Tephrosia Conzattii* is found in the appearance of 22 chromosomes plus 2 fragments in dividing cells of one seedling root-tip (Plate 1152, fig. 7). A second root-tip had 22 apparently "normal" chromosomes.

## LONGEVITY OF SEEDS

Incidental to securing root-tips for chromosome-counts, a few data concerning the longevity of seeds of *Tephrosia*, *Cracca* and *Sphinctospermum* have accumulated. The results from herbarium-collections are given in Table 2; freshly collected seeds usually give almost 100 per cent germination. While the quantities of seeds employed are too small to be statistically significant, the results are interesting in that they conform to the findings of Becquerel, Ewart, Turner, Schelderup-Ebbe and others that seeds of Leguminosae are relatively resistant to ageing and retain the power of germination for long periods.

It is of interest to note that the seeds used in the present experiments were taken from specimens which, at least in the Gray Herbarium, have been stored for the periods indicated in a very dry, steam-heated building. These have, in addition, been fumigated with carbon bisulfide at least twice. That any seeds at all germinated attests to the impervious nature of the seed coats.

In the fall of 1948, 15 seeds of *Tephrosia potosina* and 5 of *T. onobrychoides* (Moore & Wood 3618 and 3616, respectively) were subjected to the heat-treatment newly initiated at the University of California to rid herbarium-specimens of insects. In this process the temperature of an insulated room containing the specimens is raised slightly above 60° C. for about 12 hours and then allowed to return slowly to normal. All insects are destroyed by this treatment, but all 20 of the fresh seeds were apparently unharmed and germinated immediately.

These data from *Tephrosia* hardly compare, however, with records of Becquerel and Ewart of old seeds kept in herbaria or seed-cupboards. Crocker (1938) has summarized their material in reviewing the literature concerning the life-span of seeds. The following are the oldest definitely known records, all from leguminous species except the last:

<i>Cassia bicapsularis</i> L.	115 years old	40%	germination
<i>Cassia multijuga</i> Rich.	158	100%	
<i>Goodia lotifolia</i> Salisb.	105	7.7%	
<i>Hovea linearis</i> R. Br.	105	17%	
<i>Nelumbo nucifera</i> L.	150	85%	

Other records of Becquerel, Ewart, Turner and Schelderup-Ebbe as given by Crocker show several additional legumes re-



TABLE 2  
Longevity of Seeds of *Tephrosia*, *Cracca* and *Sphinctospermum*

Species	Collection	Year	Age at test	No. tested	No. germinated	% germination
* <i>Tephrosia tenella</i>	Hinckley 2959 (GH)	1944	3 yrs.	3	3	100
* <i>T. tenella</i>	Gentry 4684 (GH)	1939	8	2	2	100
<i>Sphinctospermum</i>						
<i>constrictum</i>	Gentry 4676 (GH)	1939	8	5	5	100
<i>T. belizensis</i>	Schultes & Reko 552 (GH)	1939	8	4	4	100
<i>T. foliolosa</i>	Gentry 5279 (GH)	1939	8	2	1	50
<i>T. cana</i>	Gentry 4366 (DS)	1939	8	1	1	100
<i>T. leiocarpa</i>	Gentry 4894 (GH)	1939	8	5	4	80
<i>T. Palmeri</i>	Gentry 3718 (MO)	1938	10	2	2	100
<i>T. nitens</i>	Hinton 11037 (GH)	1937	10	2	1	50
<i>T. rhodantha</i>	Hinton 11641 (GH)	1937	10	5	5	100
<i>Cracca</i> sp.	Hinton 8740 (GH)	1935	12	4	3	75
<i>T. Conzattii</i>	Hinton 6998 (GH)	1934	13	5	1	20
* <i>T. noctiflora</i>	Archer 2557 (GH)	1934	13	5	2	40
<i>T. multifolia</i>	Calderón 2611 (F)	1933	15	6	5	83
<i>T. grandiflora</i>	Orcutt 3235 (UC)	1927	21	6	4	66
<i>T. multifolia</i>	Standley 20463 (GH)	1922	25	10	1	10
* <i>T. vicioides</i>	Purpus 8171 (GH)	1918	29	13	6	46
* <i>T. Senna</i>	Rose et al. 3228 (GH)	1913	34	3	2	66
<i>T. multifolia</i>	Rose, Standley & Russell 14227 (GH)	1910	37	9	1	11
<i>T. Sinapou</i>	Pringle 11436 (GH)	1903	44	4	2	50
<i>T. leiocarpa</i>	Pringle 11434 (GH)	1903	44	1	0	0
<i>T. leucantha</i>	Palmer 745 (GH)	1898	49	4	0	0
<i>T. leiocarpa</i>	Palmer 594 (GH)	1886	61	7	0	7
	Palmer 594 (US)	1886	62	8	1	

\* Styles glabrous.

taining the power of germination after 80 years. Species with a known life-span of over 50 years include representatives of the Iridaceae, Cannaceae, Tiliaceae, Malvaceae, Euphorbiaceae, Convolvulaceae and Labiatae.

From casual observation the unsuccessful germination of *Tephrosia* seeds appeared in many instances to be due to the failure of the hypocotyl and radicle to grow. The cotyledons often remained firm and alive and in some cases expanded and became green in sunlight.

#### MORPHOLOGY AND TAXONOMIC CRITERIA

As with many genera of Leguminosae, *Tephrosia* is not distinguished by an abundance of readily utilizeable taxonomic

characters. Many parts of the plant are so variable or differ so little from one species to another that no taxonomic value can be assigned to them. Although one plant may differ from another in appearance, the problem has been one of establishing such differences on firmly objective bases. To this end as many aspects of the plant as possible have been examined. The criteria which, as a result, have been chosen are, in large part, different from those used by Rydberg and other American authors. A surprising number of characters have been found in the flowers in spite of their apparently uniform papilionaceous structure. Other characters are located in the inflorescence, fruit and some of the vegetative parts, notably the leaves. No single criterion, however, can be employed throughout the genus, so that specific delimitations are usually on the basis of varying sets of characters from one group of species to another. Notes on morphology apply primarily to the species dealt with in this revision, although much of this material will apply as well to the species with glabrous styles.

*Habit.*—All of the American species are perennial, although \**Tephrosia tenella* apparently flowers the first year from seed and may sometimes behave as an annual plant. Both herbaceous and fruticose types are included, but almost all species are somewhat woody at the base, the herbaceous types springing from a woody crown. The erect, decumbent, or prostrate habit may be of diagnostic value, but such information is seldom included on herbarium labels. *Tephrosia chrysophylla*, for example, is always completely prostrate, but in a presumed hybrid of this species with *T. florida* the stems are prostrate while the leaves are usually ascending.

Branching of the herbaceous species is either monopodial or sympodial, but this character does not seem to be of any very fundamental importance. (See *Inflorescence* and RELATIONSHIPS.)

*Roots.*—A heavy, woody tap-root is present in many species, but is not often collected. In *T. hispidula* this is characteristically carrot-like, in contrast to the cylindrical roots of *T. florida* and *T. spicata*, species with which it is sometimes confused. The roots of *T. virginiana* are many, long, slender, very tough and account for the popular names “cat-gut” and “devil’s shoestring”.

*Leaves.*—In all of the American species the leaves are im-

paripinnate with from one to forty-one leaflets, the leaflet-number varying within definite limits in each species. In seedlings the lowermost leaves are few-foliolate, but the leaflets increase in number with each successive leaf until a specific limit is reached. The same is, to a large degree, true of leaves produced by older plants within a season.

*Petioles* are usually present on at least some of the leaves, but the length of the petiole generally decreases from the lower leaves upward. Length is, therefore, usually of little value as a diagnostic character, although it is important in distinguishing the putative hybrid, *T. chrysophylla*  $\times$  *T. florida*, from its parents, both of which are extreme types. The rachis and sometimes the petiole are channeled on the upper side.

The *leaflets*, which range from narrowly linear to orbicular, from 0.5 to 18 cm. long, and from membranous to thick and leathery, are important points of recognition, once the range of variability has been determined.

More or less prominent parallel lateral veins are given off obliquely from the midrib of the leaflet in all species. The areoles formed by the veinlets between these veins are, with a few intermediate exceptions, either elongate or nearly isodiametric. This feature might appear to be correlated to some extent with the shape and width of the leaflet, but this is not necessarily so, as is evidenced by several pairs of species with leaflets of approximately the same shape and size but areoles of different shapes. The venation-type, which is usually constant within a species, is summarized in Table 3. With the exception of the few somewhat confusing intermediates, the shape of the areoles is a useful character and is, in general, correlated with the presence or absence of stomata in the upper epidermis. It will also be noted from Table 3 that these types seem to run in series of related species (which, incidentally, were determined on the basis of gross morphology before these features were studied in detail).

The presence or absence of stomata in the upper epidermis appears to be characteristic of many species. It almost goes without saying, however, that such an anatomical feature needs much more careful study with emphasis on the effect of environmental fluctuations before much dependence can be placed on it as a specific character. Nevertheless, in at least some species

this seems definitely to be a constant characteristic. The stomata of most of the species with dull, thin leaves can be seen under a strong dissecting microscope as light flecks in the dried leaflet-tissue. In these species stomata are invariably present in the upper epidermis.

Stomata are completely absent from the upper epidermis of a number of species with more or less coriaceous leaves, although in other species they may be present along the midrib only, while in still others they may be either present or completely absent (Table 3).<sup>1</sup> The presence or absence of stomata supplies a useful supplementary character (although one which will hardly be employed enthusiastically by most taxonomists, including myself) in distinguishing between *Tephrosia Pringlei* and *T. Seemannii* and to lesser extent between *T. Langlassei* and *T. simulans*. Without exception, in all the specimens I have seen, stomata are present in the upper epidermis of *T. Pringlei* but completely absent from that of *T. Seemannii*. This difference is correlated with elongate areoles between the lateral veins of *T. Pringlei* and nearly isodiametric areoles in *T. Seemannii*.

All leaflets are petiolulate and probably exhibit turgor-movements, particularly in connection with changes in light-intensity. Sleep-movements and orientations of the leaflets in sunlight have been observed in *\*Tephrosia cinerea*, *\*T. tenella*, *T. belizensis*, *T. nicaraguensis*, *T. rhodantha* and *T. spicata* and probably occur in all species. One specimen of *T. multifolia* (*Mexia 1113*) is noted on the label as exhibiting a slight sensitivity to touch. Stipels are always absent.

*Stipules* vary from setaceous to lanceolate and are either deciduous or persistent and brown or green in all the endemic species. The conspicuous, ovate, brown or reddish stipules of *T. grandiflora*, a native of South Africa naturalized in Jamaica, are a notable exception. In general stipules are too uniform, exhibiting the same variations from one species to another, to be of much diagnostic value.

<sup>1</sup> Large pieces of epidermis and cuticle of species with relatively rigid, coriaceous leaflets may conveniently be removed from leaflets of herbarium specimens by the method recommended by Bailey and Nast (1948). Leaflets are first boiled in water and then macerated in equal parts of 5% nitric and 5% chromic acids at 56° C. Two to four hours are sufficient for most *Tephrosia* species, depending upon the thickness of the leaflets. This method is unsatisfactory with thin-leaved species, such as *T. virginiana*, *T. Sinapou*, *T. spicata*, etc.

TABLE 3

Areoles, Stomata and Glands of Indigenous American Barbistyled Tephrosias

	Isodiametric (+), elongate (-), or intermediate ( $\pm$ ) areoles between lateral veins of leaflets	Presence (+) or absence (-) of stomata in upper epidermis of leaflets	Presence (+) or absence (-) of glands on <u>Leaflets Legume</u>	
1. <i>T. multifolia</i>	-	+		
2. <i>T. foliolosa</i>	-	+		
3. <i>T. macrantha</i>	-	+		
4. <i>T. Sinapou</i>	-	+	-	+
5. <i>T. leiocarpa</i>	-	+		
6. <i>T. Conzattii</i>	-	+		
7. <i>T. cuernavacana</i>	-	+		
8. <i>T. leucantha</i>	-	+		
9. <i>T. Thurberi</i>	-	+		
10. <i>T. virginiana</i>	-	+		
11. <i>T. onobrychoides</i>	-	+	-	+
12. <i>T. rhodantha</i>	-	+	-	+
13. <i>T. cana</i>	-	+		
14. <i>T. Palmeri</i>	-	+		
15. <i>T. Rugelii</i>	-	+		
16. <i>T. spicata</i>	-	+	-	+
17. <i>T. hispidula</i>	-	+	-	+
18. <i>T. florida</i>	-	+	-	+
19. <i>T. chrysophylla</i>	-	+		+
20. <i>T. tepicana</i>	+	+		
21. <i>T. madrensis</i>	+			
22. <i>T. Lindheimeri</i>	-	+	-	-
23. <i>T. potosina</i>	- , $\pm$	+	-	-
24. <i>T. saxicola</i>	+ , $\pm$	+ , -	+	
25. <i>T. Seemannii</i>	+	-	- ?	
26. <i>T. Pringlei</i>	-	+	+	
27. <i>T. nicaraguensis</i>	+	-		- ?
28. <i>T. submontana</i>	+ , $\pm$	-	+	
29. <i>T. nitens</i>	-			
30. <i>T. hypoleuca</i>	?			
31. <i>T. vernicosa</i>	+	-	+	
32. <i>T. pogonocalyx</i>	+	+ , -	+	
33. <i>T. belizensis</i>	- , $\pm$	-	+	+
34. <i>T. mexicana</i>	+ , $\pm$	+ , -	+	+
35. <i>T. Langlassei</i>	+	+ , -	+	
36. <i>T. simulans</i>	+	-	+	
37. <i>T. quercetorum</i>	+ , $\pm$	+	+	
38. <i>T. Watsoniana</i>	+	- , +	- ?	
39. <i>T. crassifolia</i>	+	+ , -	+	
40. <i>T. lanata</i>	+	-	+	
41. <i>T. Abbottiae</i>	+	- , +	+	- ?
42. <i>T. pachypoda</i>	+	-		
43. <i>T. major</i>	+	-		
44. <i>T. diversifolia</i>	+	-		
45. <i>T. platyphylla</i>	+	-		

*Indument.*—The indument is of appressed, spreading, recurved or retrorse, simple bicellular trichomes, varying in length from about 0.1 mm. to 3 mm. These hairs are often somewhat bullate with the short basal cell slightly enlarged. Trichomes are present at least on the lower surfaces of the leaves, on the pedicels, the calyx, the back of the banner and the upper suture of the ovary. The hairs are often twisted and curled in four species with very large and coriaceous leaves.

Small, flat, obovate or club-shaped glandular hairs composed of 8–10 cells in a single layer occur on the leaflets and legumes of some species. These are so inconspicuous as to pass unnoticed even under a powerful dissecting microscope and unfortunately it was not until near the end of this study, when the epidermis of leaflets was examined under a compound microscope, that these were noticed. As a result, the distribution of the glands has been only partially determined (Table 3).

The wide variation in the use of terms descriptive of pubescence makes it desirable to attempt a redefinition and reapplication of most of these, at least for the purposes of this paper. It seems particularly desirable to distinguish between the “morphology” of the indument (i. e., the nature of the individual hairs and the way in which they are arranged) and the over-all effect of the pubescence. (See Constance 1949.)

In describing the morphology of the indument, six terms are most frequently used here. These indicate the approximate length of the trichomes and whether they are appressed or spreading. Strigillose, short-strigose and strigose designate appressed hairs, while the parallel series, hirtellous, hirsutulous and hirsute, indicates ascending or spreading hairs. There is, of course, no sharp line between the various lengths, but, as delimited below, these terms have proved to be of definite value.

*Strigillose* and *hirtellous*: with minute trichomes 0.1–0.5 mm. long.

*Short-strigose* and *hirsutulous*: with trichomes about 0.6–1.5 mm. long.

*Strigose* and *hirsute*: with trichomes more than 1.5 mm. long.

*Tomentose*: the indument dense, composed of relatively fine, twisted or tortuous hairs, somewhat tangled together and matted. This type occurs chiefly in *T. pachypoda*, *T. major*, *T. diversifolia* and *T. platyphylla*.

*Villous*: the indument of soft, often somewhat twisted, but not matted, spreading hairs more than 2 mm. long.

The terms sparse, thin, moderate and dense, although admittedly indefinite, have been employed to indicate the relative abundance of pubescence in connection with the terms above.

Such terms as sericeous (or silky), pilose, lanate (or woolly), velutinous (or velvety), shining, dull, canescent and soft are descriptive of the over-all effect of the pubescence and have been employed only in a supplementary descriptive capacity.

As a taxonomic character, pubescence was greatly over-emphasized by Rydberg, and this factor alone accounts for much of the difficulty in the use of his keys. In many species, the pubescence of the vegetative parts is either spreading or appressed and is of varying lengths. Several pubescence-types often occur within the same colony, yet some of these have been given specific or varietal rank. (See the accounts of *Tephrosia onobrychoides*, *T. spicata* and *T. virginiana*.) In some instances, however, the nature of the pubescence is a useful character in conjunction with other features of the plant. The retrorse hairs of *Tephrosia Thurberi* are, for example, correlated with very narrow, but deciduous, bracts and provide a valid criterion in the determination of fruiting specimens from which the bracts have fallen. In general, the indument of vegetative parts is variable and must be used with caution.

The pubescence of the legume and of the calyx is in some cases more stable. The length of the hairs on the ovary and legume provides a simple method for distinguishing *T. hispidula* from depauperate specimens of *T. florida*. *Tephrosia foliolosa*, a very poorly known species, is separable from *T. multifolia* by minute pubescence, all of one length, on the calyx. That of *T. multifolia* is double, both hirtellous and hirsutulous or strigillose and short-strigose.

*Inflorescence*.—The structure of the inflorescence is one of the most distinctive features of the genus. Inflorescences are characteristically “racemose” in appearance with the flowers either in 2’s or, more commonly, in clusters or “fascicles” at one to fifty nodes. Each of these clusters is borne in the axil of a leaf or of a *primary bract* homologous with a leaf.<sup>1</sup> A cluster is composed

<sup>1</sup> The inflorescence of *Tephrosia Rugelii* shows varying degrees of the reduction of a multifoliolate leaf to a lanceolate bract. In this species, at least one and often as many as five flowering nodes of the inflorescence bear leaves. On some plants the lowermost of the leaves is an apparently normal vegetative leaf with from 9 to 15

of two to seven, or more, crowded flower buds, each of which is subtended at the base of the pedicel by a secondary bract.<sup>1</sup>

At least two of the buds at a node flower, while one or more may remain rudimentary. In the instances in which only two buds are present at a node, both of these flower simultaneously and anthesis proceeds centrifugally, as in *Tephrosia virginiana*, *T. Thurberi*, *T. leucantha* and *T. cuernavacana*. In those species in which 3 to 5 flowers are produced at each node, however, one of the lower buds on either side of the primary bract may open first, or both may flower together, to be followed by the third bud which lies directly behind the primary bract, and then by one or more others. In these species the flowering along the inflorescence-axis is more or less irregular, neither centrifugal nor centripetal, with the various nodes behaving somewhat independently of one another.

Although the inflorescences of many species are long and wand-like with well separated nodes, shortening occurs in varying degrees in some members of the genus. In *Tephrosia virginiana* and its allied species, the buds at a node are reduced to two plus a minute rudiment between them, and the nodes of the inflorescence are often very close together and strongly buttressed below. A similar extreme is encountered in *T. platyphylla* in which the inflorescences are very short and the buds few, while the leaflets are reduced to one or three. The inflorescence of *T. grandiflora* is composed of few flowering nodes (3 to 5), each with two functional buds and no external trace of the secondary bracts. The primary bracts are large, colored and deciduous.

The structure and flowering behavior of the inflorescence of the American species of *Tephrosia* lead to the conclusion that each cluster of buds in the axil of a primary bract or leaf represents an axillary branch-system in various degrees of reduction. Each

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leaflets. At successive nodes upward, however, the leaflet-number is reduced, eventually to a single, petiolate leaflet still with stipules at the base of the petiole. At still higher nodes the leaf and stipules sometimes appear as a deeply three-cleft bract. Eventually a single, lanceolate primary bract is found. Although all of these stages do not always occur, they do provide indications of reduction.

<sup>1</sup> Although the secondary bracts are in varying degrees smaller than the primary bract, in some instances the two outermost are nearly as conspicuous as the primary and may appear to be the stipules of the leaf represented by the primary bract. Cleared preparations, however, clearly show that the vascular traces of the secondary bracts are associated with those of the buds they subtend and not with those of the primary bracts.



“raceme” would then represent a complicated inflorescence, the component parts of which are more or less reduced and shortened.

The *position of the inflorescences* is usually constant in well-developed plants of a species. Three general types may be distinguished. Inflorescences may be (1) terminal or terminal and with shorter branches from the axils of the upper leaves, the terminal inflorescence being best-developed, (2) axillary or primarily so, with the axillary inflorescences first and best developed, or (3) apparently opposite the leaves and terminal (sympodial).

The first type is characteristic of 34 of the 49 species. Axillary inflorescences in this type are usually borne singly, although in *T. foliolosa* and *T. multifolia* two inflorescences are sometimes seen at one node. *Tephrosia multifolia* is somewhat doubtfully placed with this group, however, for although some specimens show well-developed terminal inflorescences, on most herbarium specimens the axillary inflorescences are evidently first and best developed.

Only axillary inflorescences are developed in *Tephrosia cuernavacana*, *T. Conzattii*, *T. lanata*, *T. crassifolia* and *T. bracteolata*. Both terminal and axillary inflorescences are sometimes developed in *T. rhodantha*, but the latter are usually first and best developed. These axillary inflorescences arise from one of the three buds which lie side-by-side in the axils perpendicular to the axis of the leaf. In *T. crassifolia* and *T. lanata* one or two short branches sometimes spring from near the base of an inflorescence or an inflorescence may be accompanied by one or two short inflorescences from the same axil.

The principal inflorescences of *Tephrosia rhodantha* and *T. bracteolata* are peculiar in that they emerge obliquely from the axils (i. e., from the side of the axil). The same type occurs in the otherwise very dissimilar \**T. vicioides* Schlecht. The growth of one of the lateral buds in the axil does not seem to be responsible for this peculiar behavior, for in *T. Sinapou* and *T. Conzattii*, at least, some of the axillary inflorescences develop from one of the lateral buds, but in all cases emerge from the axil in the ordinary fashion.

In the third (sympodial) group of species, in which the inflorescences are apparently opposite the leaves or terminal, the inflorescences are actually terminal but may be overtopped by the

strong growth of an axillary branch which produces another terminal inflorescence and an axillary branch. This process may be repeated several times.

Although much has been made of the monopodial versus sympodial method of branching in *Tephrosia*, the distinction between the two is frequently finely drawn, with the additional complication of the two types of axillary inflorescences. It is, for example, frequently quite difficult to determine whether a plant of *Tephrosia onobrychoides* is monopodial or sympodial and this same difficulty is one of the limiting factors in the study of the glabrous-styled species. There is also the striking example of *T. Rugelii* which is monopodial in habit, but undoubtedly most closely related to species of the southeastern United States which are definitely sympodial. A further complication is the occurrence of oblique axillary inflorescences in very dissimilar species in the glabrous- and bearded-styled groups. Monopodial versus sympodial seems to be neither a very usable nor fundamental character within the genus as a whole.

*Primary bracts* may be either persistent or deciduous and vary from subulate or setaceous to broadly ovate or oval and inflated. These bracts are important taxonomic characters in some instances. Secondary bracts are usually smaller and narrower and are generally of little diagnostic importance.

*Bracteoles* are rarely present at the base of the calyx or on the pedicels but are regularly encountered in four very different species: *Tephrosia cana*, *T. diversifolia*, *T. Abbottiae* and *T. pogonocalyx*. One to three linear to subulate bracteoles may sometimes be found on the pedicels of *T. virginiana* and *T. Thurberi*, also.

*Pedicels* vary in thickness from one species to another, but characteristically elongate somewhat and thicken in fruit. Pedicel-length is a reliable character only in widely separated species.

*Calyx*.—The five-lobed calyx is persistent in all American species except \**T. sessiliflora*, an anomalous plant in which the calyx is circumscissile at the base after anthesis. The upper lobes are usually shorter than the lowermost and are more or less united. Although in the past emphasis has been given to the length of the calyx-lobes and -tube, variation is found in the

length of the lobes within a species, so that care must be taken to include the full range. The length of calyx-lobes is, however, a useful character. Ratios of length of lobes to calyx-tube are variable, difficult of application and of little value, although the genus has been divided into subgenera partly on this basis (see RELATIONSHIPS). Shape of the lobes is relatively constant in most cases and furnishes an important taxonomic character.

*Corolla*.—All five petals of the papilionaceous corolla are clawed. The length of the claw is in some instances characteristic of a species. The banner is generally suborbicular to obovate and, in all of our species, more or less hairy on the back. A yellowish-green, apparently glandular area is present at the base of the blade within, but is frequently difficult to see in herbarium material and is seldom reported.

The wing-petals vary from oblong to obovate; the shape is not reliable. A small basal auricle is often present on the upper side of the blade near the base. The keel-petals, which are united at the outer end, may be with or without a basal auricle. For the purposes of corolla-measurement the keel is most satisfactory, for it is usually damaged least in drying and is relatively constant in length. Wings and keel are lightly coherent near the base of the blades; both are glabrous.

*Corolla-color* is seldom reported, but offers interesting possibilities. However, a tendency for a color-change to occur as the flowers age necessitates careful field-observation. Apparently in all of the species with a free vexillary stamen and in *T. onobrychoides* the corolla is white (or yellowish on the back of the banner), becoming pink and then carmine with age or violet in drying. The flowers of *T. leucantha* and *T. Thurberi* are white, becoming violet in age, while those of the related *T. virginiana* are bicolored with white or yellowish banner and rose wings and keel as, perhaps, are those of *T. nicaraguensis*. In contrast, the flowers of *T. Abbottiae* and three closely related species appear to be rose-purple, showing little or no change with age. The same is true of the peculiar pair of species, *T. Lindheimeri* and *T. potosina*, which have no evident close relatives. A number of other species show this same type of coloration. Data on specimens of *Tephrosia Sinapou* are confusing, but the few growing plants I have seen bore white flowers with violet markings on the

upper side of the wings near the base. The flowers of most of the glabrous-styled American species appear to be rose-purple or Liseran purple (Ridgeway) but at least one introduced species of this relationship seems to have white flowers.

*Androecium*.—The stamens are either monadelphous with the vexillary (uppermost) stamen free only at the base, or diadelphous with the vexillary stamen completely free from the other nine. This distinction is relatively constant and is usually observed without difficulty, although a few cases are somewhat dubious, mostly for lack of material (*Tephrosia madrensis*, *T. tepicana* and *T. bracteolata*). Interestingly enough, most of the relatively small group of diadelphous species (which have herbaceous habit and white flowers) seem to be rather closely related to each other, more so than to other members of the genus.

A more or less prominent, often two- or three-lobed thickening is frequently observed on the upper side of the vexillary stamen near the base. The margins of the staminal tube on either side of this callosity are also thickened, sometimes conspicuously so, as in *T. macrantha*, in which a knob-shaped structure is present.

Filaments and anthers are unappendaged. The anthers are uniform in size and arranged in two equal, alternating series, one above the other.

*Gynoecium*.—The sessile ovary is surrounded at the base within the staminal tube by a saucer- or collar-like disc characteristic of the Subtribe Tephrosiinae of the Tribe Galegeae. Four to sixteen ovules are borne along the upper suture, alternating ovules being attached to either valve. Ovule-number exhibits characteristic variations which are more or less clearly reflected in seed-number. There appears to be a tendency toward reduction in ovule-number in the genus. The 10 to 16 ovules of *T. rhodantha* distinguish it from other species of its group, while *T. Lindheimeri* and *T. potosina* at the other extreme bear but from 4 to 8. Among the smooth-styled species, \**T. cinerea*, with from 10 to 12 (rarely as few as 8) ovules, is readily separated from other species, with 6 to 8.

The style may be glabrous or barbate with fine white hairs along the inner (upper) side. In all of the species with which this revision deals the style is more or less barbate. The glabrous-styled group includes all of the species with small

purple flowers, such as *\*T. cinerea*, *\*T. tenella* and *\*T. Senna*, as well as the very aberrant *\*T. sessiliflora*. In all species the stigma is terminal, small and penicillate. Tufts and rings of hairs are absent from the style.

*Fruit*.—In all of the American species, the two-valved, strongly dehiscent legume is essentially linear and most often nearly straight, although an upward or downward curvature is exhibited by several species. One to four pods are borne at a flowering node. Those of *T. macrantha* and *T. multifolia* characteristically droop, while all others are ascending or spreading. The persistent style-base forms distally on the upper side of the legume a more or less prominent beak which effectively distinguishes the legume of *Tephrosia* from the equally tapered pods of *Galega*. Pubescence, width and length of the legume and the number of seeds are the most useful characteristics, provided fully developed pods are chosen. Pubescence is, however, sometimes deceptive. A layer of elongated, thick-walled cells arranged diagonally below the epidermis gives the ripening legume the striate appearance remarked by Rydberg (1923) and apparently is responsible for the rupture of the ripe pod and the coiling of the valves.

*Seeds*.—The seed-coats of all of the indigenous species are smooth and usually of various shades of brown or gray, variegated with black. Two notable exceptions are the closely-related *T. Lindheimeri* and *T. potosina*, the seeds of which are buff or stramineous and unmarked. In the introduced species, *\*T. noctiflora*, the seed-coat is reddish brown and strongly wrinkled. The large, flat, black seeds of another introduced species, *T. Vogelii*, bear a conspicuous white caruncle, which is seen to a lesser degree in the related species, *T. candida*. In other species the caruncle is usually inconspicuous. Characteristic variations in seed-shape from subspherical to cylindrical to compressed and more or less reniform in outline occur, but crowding within the pod strongly influences both shape and size. The subglobose seeds of *T. chrysophylla*, *T. florida* and *T. spicata* contrast markedly with the cylindrical seeds of *\*T. tenella* and *\*T. cinerea* or those of *T. Vogelii*, *\*T. noctiflora*, *T. Lindheimeri* or *T. potosina* mentioned above. Comments on the internal morphology of the seeds of several species have been published by Martin (1946).

## MEASUREMENTS

All measurements included in the descriptions of species have been taken directly from dried herbarium-material, with the exception of those involving flower-parts. The data relative to flower-parts are either from specimens preserved in alcohol or from flowers expanded by boiling. Length of the dried flower as encountered in herbarium-material has been indicated in most instances, but is not significant in more than a general way, since the petals (in particular the banner) often crumple or shrink in drying.

Length of the *inflorescence* includes the peduncle between the lowermost flowering node and the next lower leaf. In most instances the length of the peduncle is noted separately as well.

*Calyx-length* has been measured in all instances along the upper side from the receptacle to the tips of the upper lobes. Length of the calyx-tube, where indicated, is measured between the upper and lateral lobes. The upper calyx-lobes are measured from the base of the sinus between them to the tips of the lobes. *All measurements of calyx-parts have been made from flowers at anthesis.* The relative proportions of the lobes, as well as their shape and length, change from bud to flower and from flower to fruit.

Length of the blade of the *banner* and of the claw are given separately since the banner is strongly reflexed, making measurement difficult. All measurements of *wings* and *keel-petals* include the claw, however. The keel is measured from the proximal tip of the claw to the apex of the keel.

The *staminal tube* has been measured along the lower side and does not include the full length of the stamens.

Length of the *legume* does not include the persistent base of the style which, in most instances, forms a beak on the upper side.

## RELATIONSHIPS

*Tephrosia*, in the sense used in this paper, is a natural genus defined on the basis of a number of characters. These include the collar-like disc surrounding the base of the ovary, the imparipinnate leaves, the simple trichomes, the terminal penicillate stigma, the unappendaged equal anthers, the pubescent back of the banner, the wings slightly coherent with the obtuse keel, the

absence of stipels, the peculiar inflorescence and the apparently uniform occurrence of 11 pairs of chromosomes. Some of these characters are shared in various combinations with presumably related genera, but others, such as inflorescence and chromosomes, set the genus apart.

Although various relationships have been assigned to *Tephrosia* within the Tribe Galegeae, this question is badly in need of critical examination in terms of the whole plant, a project far beyond my present scope. In order to give a general idea of likely relationships, however, it may be noted that Taubert (1894) placed *Tephrosia* in the Subtribe Tephrosiinae along with *Galega* L., *Ptychosema* Benth., *Sylitra* E. Mey., *Mundulea* DC., *Millettia* Wight & Arn., *Wisteria* Nutt., *Fordia* Hemsl., *Sarcodum* Lour., *Platysepalum* Welw., *Poecilanthe* Benth., *Chadsia* Boj., *Barbieria* DC., *Peteria* A. Gray, *Poissonia* Baill. and *Bolusia* Benth.

Rydberg (1923a), considering the North American representatives of this group, divided the Tephrosiinae into two subtribes, the Craccanae, including *Galega*, *Cracca* L. (= *Tephrosia*) and *Peteria*, and the Millettianae with *Kraunhia* Raf. (= *Wisteria*). The general reliability of this bit of classification may be judged by Rydberg's statement regarding *Barbieria* which he placed in a subtribe of its own considerably removed from the Craccanae and Millettianae: "The Tephrosieae of Bentham (Tephrosiinae of Taubert) is in itself not a natural division, for *Barbiera* is not at all closely related to the rest, being distinguished by the long-clawed petals, the presence of 2 bractlets beneath the tubular calyx, and the style bearded along the upper side." This general idea may possibly be true, but the evidence presented is hardly convincing, for there are 45 endemic American species of *Tephrosia* with bearded styles and 4 of these bear bracteoles on calyx or pedicels.

*Tephrosia* itself has been variously divided into sections, but until much more of the Old World material can be examined it seems neither feasible nor wise to attempt to establish further formal subgeneric groups, although it is certain that a realignment will be necessary. It may, nevertheless, be worthwhile to indicate some of the possible subdivisions.

It appears to me that two principal divisions within the genus must be based on glabrous styles versus barbate styles. Although this may seem to be an arbitrary division based on a single character, it is perhaps the same type of distinction as the presence or absence of chaff or bristles on the receptacle of the Compositae which sets off large and presumably related groups of genera. Such a split in *Tephrosia* is apparently fundamental within the New World species, at least, as is borne out by related species which lead from one small group of species to another (although there are gaps). In general, the two series are composed of very different species and parallel series are not found in the two divisions, although such features as unifoliolate leaves, sympodial branching, oblique axillary inflorescences and similar flower-color may appear in otherwise quite dissimilar species.

It may also prove desirable to recognize a small, closely knit barbistyled group of species of southern Africa which includes *Tephrosia grandiflora* and its allies with large stipules and ovate, spathaceous primary bracts. Secondary bracts are completely absent. This alliance has been designated Section *Apodynomene* (E. Mey.) Harvey, Fl. Capensis **2**: 203. 1861.

There are at least two other small groups which are probably not worth recognition, but with which I am poorly acquainted. These are the sections (or genera) *Pogonostigma* and *Requienia* which include a few African species with 1-seeded fruits. The leaves of the first are compound, those of the second unifoliolate. Should these prove to be worthy of the sectional rank assigned them by Taubert, the remainder of the genus may well be designated *Eutephrosia* Harvey, Fl. Capensis **2**: 203. 1861.

The main body of the genus (*Eutephrosia*, including both barbate- and glabrous-styled species) has customarily been divided since the time of DeCandolle into the Sections *Brissonia* (Moench) DC. and *Reineria* (Neck.) DC., but these are artificial groups based upon a combination of habit (monopodial vs. sympodial) and the ratio of length of calyx-lobes to -tube, characters which are not necessarily correlated with one-another. (See MORPHOLOGY: *Habit*, *Calyx* and *Inflorescence*; also Rydberg 1923a.) Rydberg (1923) established 17 small, completely new sections for the North American species, but some of these are



manifestly artificial and none can be rearranged or retained satisfactorily in terms of the whole genus.

Although it would be gratifying to be able to set down a chart showing the phylogeny of the American barbistyled species, the interrelationships of these plants are far from clear. Some small groups or pairs of species are clearly related to each other, and the group as a whole may be divided into two main complexes, but even after this there are a number of species apparently not very closely related to each other or to any of the small groups. The interrelationships of the latter are not very clear, either.

It must, as a result, suffice to point out that the American species fall into two principal series. The plants of the first series (A) (including Species 1 to 23) possess thin leaflets bearing stomata in the upper epidermis. The areoles between the principal parallel lateral veins are distinctly elongate. The second series (B) (Species 24 to 45) includes species with either thin or very coriaceous leaflets, generally with nearly isodiametric areoles between the lateral veins of the leaflets, and usually with few or no stomata in the upper epidermis. A strong tendency toward reduction in the number of leaflets is encountered in this series and the flowers of most of the species seem to be rose-purple.

Within Series A, two distinct subdivisions may be recognized, according to the coherence of the vexillary stamen with the staminal tube. In five closely related species of the southeastern United States, in the two species occurring in Baja California, in *Tephrosia tepicana* and in *T. madrensis* from the Sierra Madre of Sinaloa and Nayarit, Mexico, and in the more widespread *T. rhodantha*, the vexillary stamen is completely free from the staminal tube, even in the smallest buds (Species 12 to 21; see Key 2). These are all herbaceous, white-flowered species which exhibit a tendency toward reduction in leaflet-number. In the remainder of the species of Series A, the vexillary stamen is coherent with the staminal tube, although free at the base. This subdivision embraces both woody and herbaceous types. The basic flower-color appears to be white, although at least *T. virginiana* has bicolored flowers and *T. potosina* and *T. Lindheimeri*, placed here although apparently not closely connected with any of the other American species, bear rose-purple flowers. A possible connecting link between the two groups of Series A is

found in the white-flowered *T. onobrychoides* of the Gulf Coastal Plain of the United States, which approaches the southeastern species in habit and general appearance but in which the vexillary stamen is fused with the staminal tube.

Various exceptions to the general characters distinguishing the two principal groups will be noted in Table 3. Within Series A the areoles of the leaflets of *T. tepicana* and *T. madrensis* are distinctly isodiametric, although stomata are present in the upper epidermis of at least the former. The material of these two is very scanty but the vexillary stamen appears to be free, thus linking them with similar members of this group. Conversely, the areoles of *T. Pringlei* of Series B are conspicuously elongate and stomata are invariably present in the upper epidermis of the leaflets, but this plant is otherwise allied to *T. Seemannii* and *T. saxicola*. Similarly, the areoles of *T. nitens* are elongate and those of a number of other species of this group are more or less intermediate in shape, although other characters clearly link them with this assemblage.

The relationships of various pairs or small groups of species, in addition to those already mentioned, are brought out in the discussions of individual species. A branching system of relationships or a brush-heap structure would undoubtedly be far more satisfactory than the linear sequence which must necessarily be used, for I suspect that woody types of Series A with relatively many leaflets and flowers at a node, such as *T. multifolia* and *T. Sinapou*, have led to more specialized forms, such as *T. virginiana*, *T. Conzattii* and *T. leiocarpa*, and have led as well to those with a free vexillary stamen and to Series B. I have, however, tried to show in their linear arrangement such relationships as seem to be indicated by the morphological features of the plants.

#### DISTRIBUTION AND ECOLOGY

The barbistyled *Tephrosias* are primarily North American in their distribution in the New World, with only *Tephrosia Sinapou* and *T. nitens* extending into South America. Outline Maps 1 to 20 indicate the distribution of individual species in North America, and this information is summarized in the accompanying Generalized Distribution Map. Such a generalized map can only indicate the total number of species known to occur in a

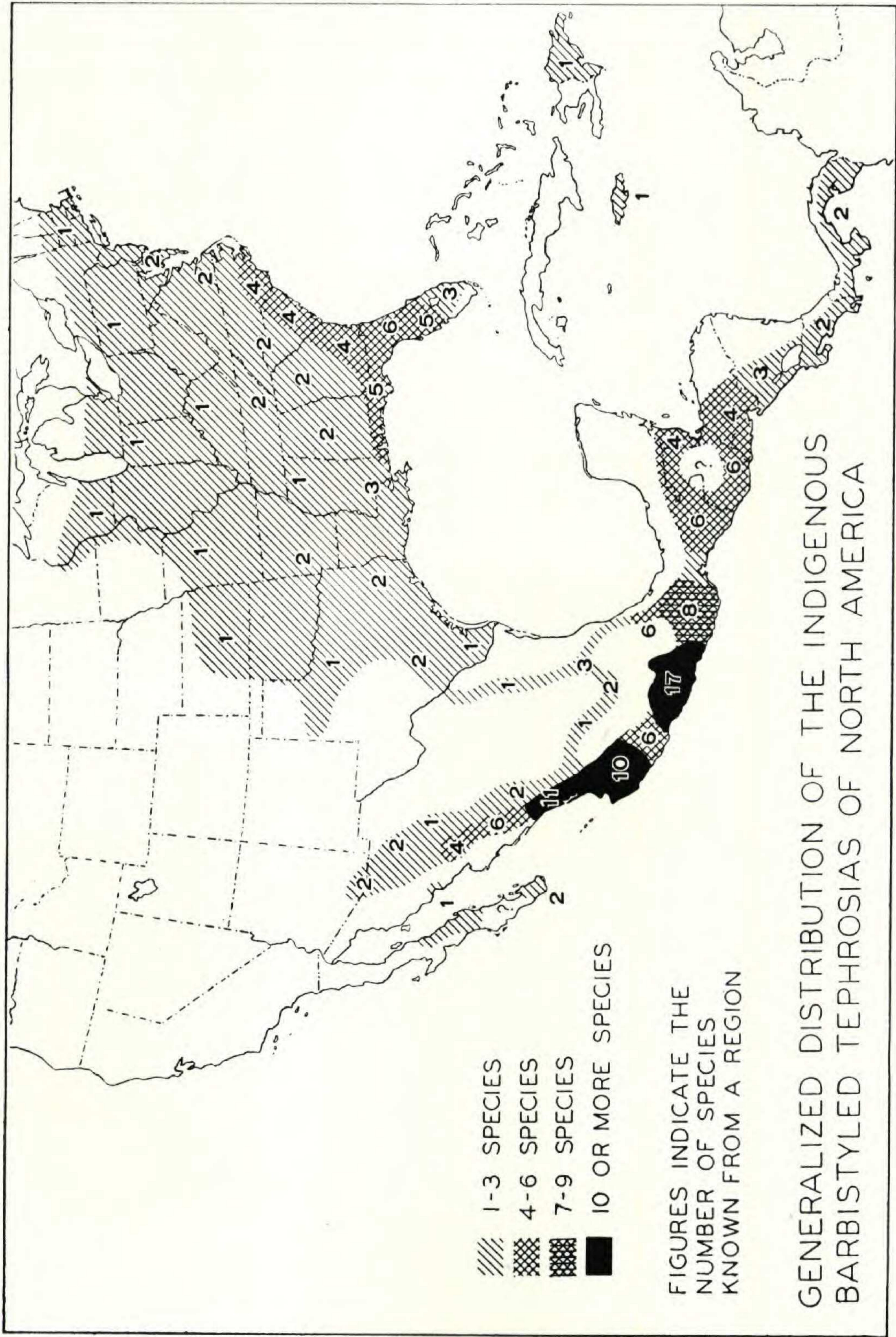
given region, since it is obvious that no two species will have the same range and that distributions will overlap in varying degrees. In addition, the number of species from some areas may be expected to change as our knowledge of Mexico and Central America increases and new species are discovered. Nevertheless, it will be seen immediately that the chief diversity of the barbistyled group is in the mountains of southwestern Mexico,<sup>1</sup> particularly in the region from southern Sinaloa to Guerrero and Morelos (areas in solid black on the map). Twenty-seven of the 45 species are known to occur in this territory and 20 of these are endemic to this area.

Within this region of concentration of species, two divisions apparently exist: a northern part consisting of southern Sinaloa, Nayarit and western Jalisco separated by Michoacán from a southern area including Guerrero, southern México<sup>1</sup> and Morelos. This southern region is in turn subdivided by the lowlands of the Río Balsas into a northern portion (southern México, Morelos and northern Guerrero) and a southern portion (the remainder of Guerrero south of the Río Balsas). Eleven barbistyled species of *Tephrosia* are known from each of these areas and a total of 17 from the two together. The decrease in concentration represented by Michoacán with only 6 species may be more apparent than real since much of the western part of the state which may be expected to harbor *Tephrosias* is as yet largely unknown botanically and otherwise.

Outside this rich band of mountainous country with 27 species the number of species declines rapidly, although some endemism is still evident, for only a few types are really widespread, extending from various parts of Mexico varying distances into Central or South America. These widespread species include *Tephrosia nicaraguensis*, *T. multifolia*, *T. nitens*, *T. Sinapou* and *T. rhodantha*.

Of the eight species known from Oaxaca, only one (*T. Pringlei*) is confined entirely to that state. The others are shared to the north, west or east. One type of distribution also seen in other genera is exemplified by *T. Conzattii*, represented from Oaxaca, Guerrero and southern México, and another in *T. Langlassei*,

<sup>1</sup> In order to distinguish between the Republic of México and the State of México, the English spelling is used throughout for the republic and the accented Mexican form for the state.



which extends both north and west and then southward into Chiapas. Still another distribution is that of *T. belizensis*, reaching from Veracruz across the northern side of Oaxaca into Chiapas and British Honduras. In Veracruz, *T. lanata*, in addition to *T. belizensis* and *T. Langlassei*, extends along the slopes of the eastern sierra southward and eastward; the other three species occurring in Veracruz are widespread.

Guatemala can claim at present only one endemic species, and that an undescribed, distinct but sterile plant collected by Steyermark in the Department of Huehuetanango (see Species 21). The other six species (the undescribed plant was omitted from the generalized map) include five widely distributed types and *T. lanata*. Southward from Guatemala the number of species decreases and only *T. multifolia* and *T. nitens* are known to reach Panama. It is strange that *T. Sinapou* has not been collected beyond El Salvador, for it has a wide distribution in South America and appears in the West Indies.

No collections of *Tephrosia* are known to me from Hidalgo, Puebla, Aguascalientes, the higher parts of México, and most of eastern and northern Jalisco and Michoacán, although two species reach the northern side of this area in the oak forests of Guanajuato and Querétaro, and one extends northward again to a corner of Tamaulipas.

Eleven barbistyled *Tephrosias* occur in the United States. *Tephrosia leiocarpa* and *T. Thurberi* reach the mountains of southern Arizona and *T. potosina* extends from San Luis Potosí into Texas, where its range meets that of the related *T. Lindheimeri*. This last species has not yet been collected in Mexico but is not uncommon in southern Texas to the Mexican border at the Río Grande.

The most widely distributed species in the United States is *Tephrosia virginiana*, which is found from New Hampshire to Wisconsin and south to Florida and western Texas. *Tephrosia onobrychoides* occupies a part of the Mississippi embayment of the Gulf Coastal Plain. The remaining five species, all plants with the vexillary stamen free, radiate more or less concentrically northward from central peninsular Florida, with *T. Rugelii* occupying the smallest and *T. spicata* the largest area, the latter extending well off the Coastal Plain. Plants presumably most

closely related to these five species occur in Baja California, western and southern Mexico, and Guatemala.

Each of these present-day distributional patterns is, of course, delimited by the area covered by the particular set of environmental conditions to which that species is attuned. Each distribution must also reflect to some degree both the history of the species and geological history. Presumably, most of these species already occupy the suitable habitats now available to them and are prevented by unfavorable environmental conditions from expanding their ranges farther. An attempt to explain distributions with only the present data from which to judge would be both premature and unwarranted, but a number of coincidences are strikingly suggestive and worth underscoring.

Although ecological notes concerning many species of Mexico and Central America are scanty or lacking altogether, it is evident that the majority of the Mexican species are confined to well-drained soils in open oak and/or pine forests in non-calcareous areas mostly below 2300 m. (ca. 7500 feet). Exceptions are found in relatively wide-ranging species such as *T. multifolia*, *T. rhodantha* and *T. nitens*, which may occur outside the oak-pine forests in open areas at low altitudes, and in *T. leucantha* of oak and pine forests southward from northwestern Chihuahua to Guanajuato and Querétaro, where it may be found at 2500 m. (8000 feet). It may be significant that the greatest diversity of the barbistyled group is in mountainous regions in which rain is lacking during winter and spring and the winters themselves are warm.

Part of the absence of the genus from Hidalgo, Puebla, Aguascalientes, eastern and northern Jalisco and Michoacán and the higher parts of México (assuming that this absence is real and not due to insufficient collecting) may be attributed to semi-desert conditions which occupy a portion of this expanse. In Hidalgo, where extensive search has failed to reveal a single species of *Tephrosia*, it is perhaps significant that oak and pine forests where *Tephrosias* might be expected to occur are primarily on soils of calcareous derivation, whereas apparently non-calcareous soils are the rule in those parts of Mexico where numerous species have been collected.

In the United States *Tephrosia virginiana*, *T. onobrychoides* and the five species of the southeastern states are always found in open habitats in non-calcareous soils. All of the stations of *T. onobrychoides* appear to occur on well-drained, leached, sandy, acid, non-calcareous red and yellow podzolic soils of the Norfolk-Ruston, Caddo-Beauregard, Hockley-Katy, Lake Charles-Crawley and Hanceville-Conway series and the species disappears abruptly when the black prairie and other Rendzina soils of the Houston-Austin-Denton and Victoria-Goliad series (derived from marls, chalks and calcareous clays) (U. S. Dept. Agr. 1938) are reached. This coincidence suggests that at the western edge of the range edaphic factors may be limiting, but that other factors at various other points on the periphery of the species may also be limiting, for suitable Norfolk-Ruston soils are widely distributed around the Coastal Plain to Virginia.

*Tephrosia Rugelii*, *T. chrysophylla*, *T. florida*, *T. hispidula* and *T. spicata*, of the southeastern United States, all occur on sandy soils of the Coastal Plain; the first four are completely restricted to that area, but *T. spicata* extends into well-drained sandy and sand-clay soils over a wider area. *Tephrosia Rugelii* occupies the smallest expanse, being found on sands of the Leon-Bladen and Norfolk-Blanton soils primarily in oak barrens in the flatwoods regions of central peninsular Florida. *Tephrosia chrysophylla* grows prostrate on open white sand in dry oak barrens over a larger range, while *T. florida* occupies a still larger area, always on sandy, but often somewhat more shaded and moister soils. An extreme is reached in *T. hispidula* which is distributed primarily in the grassy and sedgy pine flatwoods along the Atlantic Coastal Plain in sandy soils of the Leon-Bladen and Coxville-Portsmouth-Bladen groups, which may be moist or even wet, in contrast to all the other species with which I am acquainted.

With all of these species the circumstantial evidence strongly suggests that edaphic factors are important in determining distribution. *Tephrosia florida* is, for example, very abundant on the Norfolk sand in Richmond County, North Carolina, in the northern part of its range, but disappears along with the long-leaf pine (*Pinus australis* Michx. f.) as the abrupt transition to the heavier Georgeville-Alamance soils occurs. As was indicated previously, almost all of the barbistyled species are known on